
A HISTORICAL AND TAXONOMIC SYNOPSIS OF RHIZOPHORACEAE AND ANISOPHYLLEACEAE¹

Adrian M. Juncosa and P. Barry Tomlinson²

ABSTRACT

Even from its time of formal recognition by Robert Brown in 1814, the Rhizophoraceae has been known as a family with both terrestrial and mangal representatives so that the tendency to regard it as the "mangrove family" is inappropriate, even though one of its major subdivisions, the tribe Rhizophoreae, is made up exclusively of mangroves. This association of terrestrial and mangrove species adds a piquancy to the study of the systematics of the group because it allows the diagnostic usefulness of "adaptive" characters to be assessed. The progressive enlargement of our knowledge of the family is reviewed, including the status of Anisophyllea and related genera, now regarded as constituting a separate family Anisophylleaceae. Brief tribal and generic diagnoses are provided, with generalized illustration of geographical distribution. Some portraiture of the more common genera is attempted.

This symposium had as an objective the segregation of the small family Anisophylleaceae from the Rhizophoraceae (sensu lato), with a discussion of the evidence upon which this distinction was based (cf. Dahlgren, this volume). A further objective has been a discussion of where the two families might be placed in a natural system. Although the mangrove Rhizophoraceae are familiar to botanists and laymen alike, the systematic characteristics and even the existence of the inland genera are not well known. The Rhizophoraceae and Anisophylleaceae together include about 18 genera and some 140 species of tropical shrubs and trees (Table 1). The families exhibit a wide variety of character states and have had a checkered taxonomic history. It seems now generally agreed that the Anisophylleaceae are a distinct, probably unrelated family; for a detailed systematic comparison see our other contribution in this volume. Unless otherwise noted, "Rhizophoraceae" is therefore used sensu stricto, i.e., without the four genera now removed as Anisophylleaceae. In addition to describing this history, we present a syn-

opsis of genera. No such complete synopsis appears elsewhere, so it should prove a useful reference for this symposium volume. A detailed comparison of the systematic and biological characteristics of the two families appears separately (Juncosa & Tomlinson, this volume).

TAXONOMIC HISTORY OF RHIZOPHORACEAE (SENSU LATO)

The family Rhizophoraceae, in a broad sense, originates with the genus *Rhizophora* of Linnaeus (1753), preceded by *Mangium* of Rumphius (1741-1755). Both of these authors used their generic names to designate a group of species growing in tropical tidal swamps, which modern ecologists would call "mangal" (Macnae, 1968). Of the seven species named by Linnaeus in *Rhizophora*, only one, *R. mangle* L., is still valid and forms the type species of the genus and hence of the family. *Mangium* has disappeared entirely, except in *Acacia mangium*, a terrestrial plant. A list of the Rumphian and Linnean names with their

¹ We thank Paul P. K. Chai and the Forest Department, Kuching, Sarawak; John S. Bunt, Norman C. Duke, and the Australian Institute of Marine Science; the Forest Department, Brunei; and the Servicio de Parques Nacionales, Costa Rica, for permission to collect and for assistance in field studies. We also thank Jack B. Fisher, Hiroshi Tobe, and Peter H. Raven for supplying material of several genera, and Monica Mattmuller and Ed Selig for technical assistance. Distribution base maps are by the University of Chicago Press. Research support has come directly from N.S.F. dissertation improvement award DEB 80-16635 to A. Juncosa and BSR 82-16271 (P. B. Tomlinson, P.I.) and a grant from the National Geographic Society to P. B. Tomlinson. Additional support has come from the Cabot Foundation and Atkins Garden Funds of Harvard University.

² Harvard University, Harvard Forest, Petersham, Massachusetts 01366, U.S.A.

TABLE 1. Summary of genera of the Rhizophoraceae (s. str.) and Anisophylleaceae (after Ridley, 1922; Alston, 1925; Ding Hou, 1958; Melchior, 1964; Floret, 1974; van Vliet, 1976; Willis, 1973; Steyermark & Liesner, 1983). Tribal classification of Rhizophoraceae follows that accepted in the literature; recent studies indicate that changes are necessary (Tobe & Raven, this volume).

Family or Tribe	Genus	Number of Species	Distribution
ANISOPHYLLEACEAE			
(= Anisophylleae)	<i>Anisophyllea</i>	25	Africa to South America and Malesia
	<i>Combretocarpus</i>	1	Borneo
	<i>Poga</i>	1	Africa
	<i>Polygonanthus</i>	2	Brazil
RHIZOPHORACEAE			
Gynotrocheae ¹	<i>Carallia</i>	9	Madagascar to Australia
	<i>Crossostylis</i>	12	South Pacific
	<i>Gynotroches</i>	1 ²	Indochina, Malesia, Pacific Islands
	<i>Pellacalyx</i>	8	Malesia to S China
Macariseae ¹	<i>Anopyxis</i>	2	Africa
	<i>Blepharistemma</i>	1	India
	<i>Cassipourea</i> (including <i>Lasi-osepalum</i> and <i>Weihea</i>)	55	Sri Lanka to Central America
	<i>Comiphyton</i>	1	Equatorial Africa
	<i>Dactylopetalum</i> ³	15	Africa, Madagascar
	<i>Macarisia</i>	7	Madagascar
	<i>Sterigmapetalum</i>	7	South America
Rhizophoreae	<i>Bruguiera</i>	6	Africa to Australia
	<i>Ceriops</i>	2	Africa to Australia
	<i>Kandelia</i>	1	Malaysia to Japan
	<i>Rhizophora</i>	8 ⁴	pantropical

¹ Tobe & Raven (this volume) segregate *Crossostylis* as its own tribe and create two subtribes each in Macariseae and their modified Gynotrocheae.

² Ding Hou (1958) described much variation in *Gynotroches* and only reluctantly accommodated it in a single species. Juncosa & Tobe (this volume) describe some characteristics of two of the several distinct taxa.

³ Floret (1976) presented evidence for the elevation of *Dactylopetalum* to generic rank.

⁴ Includes putative hybrids or varieties (Tomlinson, 1986).

modern equivalents forms Table 2. This demonstrates an intrinsically ecological concept for their initial circumscription.

The family was formally designated (as the "order" Rhizophoreae) by Robert Brown in his account of the botany of Terra Australis (Brown, 1814) and included the genera *Rhizophora* Linnaeus, *Bruguiera* Lamarck, and *Carallia* Roxburgh "all of which are found in the equinoctial part of New Holland." Consequently, even at its erection the family already included plants of terrestrial as well as mangal habitats. Robert Brown drew attention to the "affinity of Rhizophoreae to Cunoniaceae" and rejected Jussieu's attempt to combine some of its elements with loranthaceous genera (cf. Dumortier, 1829). The subsequent development of our knowledge of the family is summarized in Table 3.

Endlicher (1840) subdivided the family into Leg-

notidae (*Cassipourea* and *Drytopetalum* = *Gynotroches*) and Rhizophoreae sensu stricto, which still included *Carallia*. Blume (1849) raised these two divisions to family status but transferred *Carallia* to Legnotidae so that the first recognition of the Rhizophoreae (not in Brown's sense) as "mangrove Rhizophoraceae," i.e., a named taxon capable of ecological designation, is from this date, even though Blume's "families" have scarcely been recognized by subsequent authors. Corner (1976) did recognize Legnotidaceae in his description of seeds of dicotyledons. Bentham & Hooker (1865), treating the Rhizophoraceae as a family, maintained Rhizophoreae and Legnotidae as tribes but added Anisophylleae as a third tribe to include the terrestrial genera *Anisophyllea* and *Combretocarpus*.

This system was essentially followed by Baillon (1876), who split the Legnotidae into two separate

TABLE 2. Present probable status of some Linnean and Rumphian names in *Rhizophora* and *Mangium* (see Salvoza, 1936).

	Present
A. <i>Rhizophora</i> Linnaeus (1753)	
<i>R. mangle</i>	<i>R. mangle</i> L.
<i>R. gymnorhiza</i>	<i>Bruguiera gymnorhiza</i> (or <i>gymnorhiza</i>) (L.) Lamk.
<i>R. cylindrica</i>	<i>Bruguiera cylindrica</i> (L.) Bl.
<i>R. candel</i>	<i>Kandelia candel</i> (L.) Druce
<i>R. caseolaris</i>	<i>Sonneratia caseolaris</i> (L.) Engl.
<i>R. majus</i>	<i>Aegiceras corniculatum</i> (L.) Blanco
<i>R. corniculata</i>	<i>Aegiceras corniculatum</i> (L.) Blanco
B. <i>Mangium</i> Rumphius (1741-1755)	
<i>M. candellarium</i>	<i>Rhizophora apiculata</i> Bl.
<i>M. celsum</i>	<i>Bruguiera gymnorhiza</i> (L.) Lamk.
<i>M. minus</i> (p.p.)	<i>Bruguiera gymnorhiza</i> (L.) Lamk.
<i>M. digitatum</i>	<i>Bruguiera cylindrica</i> (L.) Bl.
<i>M. minus</i> (p.p.)	<i>Bruguiera cylindrica</i> (L.) Bl.
<i>M. caryophylloides</i>	<i>Bruguiera cylindrica</i> (L.) Bl.
<i>M. caryophylloides</i> <i>parvifolium</i>	<i>Ceriops tagal</i> (Perr.) C. B. Rob.
<i>latifolium</i>	
<i>M. caseolare rubrum</i>	<i>Sonneratia caseolare</i> (L.) Engl.
<i>M. floridum</i>	<i>Aegiceras floridum</i> R.&S.

tribes, Macariseae and Barraldeieae (= Gynotrocheae) from *Barraldeia* (= *Carallia*). Ridley (1922) raised the three tribes to families (his "orders," viz. Rhizophoraceae, Legnotidae, and Anisophylleae) but considered only the Malayan genera.

Schimper (1898) retained the traditional one-family concept but departed dramatically from the general consensus by splitting the family on morphological characters that he considered to be more fundamental than the structure of the fruit and seedling, since he considered their specializations to be features adapting the plants to their habitat (Anpassungsmerkmal) and therefore comparable to those found in other isolated mangrove taxa like *Aegiceras*, *Avicennia*, *Lumnitzera*, and *Sonneratia*. This may be seen as a complete reversal of the Linnean view. Schimper developed an elaborate subdivision, cutting across ecological characteristics as follows:

subfamily I. Rhizophoroideae

tribe 1. Gynotrocheae

subtribe 1a. Gynotrochinae [*Crossostylis* (as *Crossostyles*), *Gynotroches*, *Rhizophora*, *Ceriops*, *Kandelia*]

subtribe 1b. Carallinae [*Pellacalyx*, *Bruguiera*, *Carallia*]

tribe 2. Macariseae [*Blepharistemma*, *Dactylopetalum*, *Macarisia*, *Weihea*, *Cassipourea*]

subfamily II. Anisophylloideae [*Anisophyllea*, *Combretocarpus*]

This arrangement has been summarily rejected by all subsequent authors, in particular it leads to Ding Hou's statement (1958), which might well be placarded in all institutes of systematic botany: "Schimper's clearly wrong classification provides again a good example of what danger is involved if a taxonomist introduces pre-occupied theoretical ideas into classification." In fairness to Schimper, it should be pointed out that he had a better idea of fruit and seed construction than most of his predecessors, since he recognized that the family Rhizophoraceae, which Brown had characterized as exalbuminous, did indeed possess well-developed endosperm (Juncosa, 1982), and that *Bruguiera* was appreciably different from the other mangrove taxa in some basic features. However, the sum of all vegetative features and especially of wood anatomy (Marco, 1935; van Vliet, 1976) shows that the habitat distinctiveness of the Rhizophoreae, even though it can be said to be primarily based upon "adaptive" or "ecological" characteristics, is well founded at the systematic level. The family therefore provides an interesting example for phyletic study since the Rhizophoreae are clearly derivative and must have had an ancestry in taxa that are now represented by the terrestrial genera. The most recent accepted intrafamilial classification (Table 1) was initially presented by Melchior

(1964). It recognizes three tribes: Macarisieae, with a center of distribution in Africa; Gynotrocheae, centered in Malesia; and Rhizophoreae, also centered in Malesia.

Monographs and partial revisions of varying utility exist for some genera of Rhizophoraceae. Alston (1925) discussed the largest genus, *Cassipourea*, including within it *Dactylopetalum*, *Weihea*, and *Lasiosepalum*. The related genus *Comiphyton* was described by Floret (1974), who subsequently discussed relationships of African Macarisieae further (Floret, 1976). *Sterigmapetalum* was recently revised by Steyermark & Liesner (1983). Several systematic treatments of *Rhizophora* or portions thereof exist (Salvoza, 1936; Ding Hou, 1960; Breteler, 1969, 1977). Yet only in the western Pacific, where the plants have been studied largely in the field rather than as dried material, is our understanding of the taxa adequate (Tomlinson, 1978; Duke & Bunt, 1979), although many basic questions about distribution, hybrids, and specific limits still remain unanswered. Excellent revisions of other Malesian genera, both mangrove and inland, are found in Ding Hou (1958). Our present understanding of the mangrove Rhizophoraceae is summarized in Tomlinson (1986).

In looking at the history of this family, one is impressed by the relative recentness of our present taxonomic and nomenclatural understanding. For example, the clarification of the full range of morphology in *Bruguiera* only comes with Ding Hou (1958); *Ceriops decandra* was correctly designated for the first time in this monograph. The difference between the two species of *Ceriops* is quite striking when floral function is considered. Some African taxa have been discussed by J. J. Floret (1976), while the New World taxa have been treated incompletely by a few authors (e.g., Prance et al., 1975).

One might conclude that any discussion of the phylogeny of this family is premature in the absence of detailed information about many species, but the situation reflects our ignorance of tropical plant families generally. If we can devote at least as much time to observation as we are doing to speculation about phylogenies, then our understanding is likely to improve.

AFFINITIES WITH OTHER FAMILIES

Rhizophoraceae (sensu lato) have traditionally been placed in the Myrtales (Bentham & Hooker, 1865; Melchior, 1964; Takhtajan, 1980), although more recently they have sometimes been aligned with Cornales (Cronquist, 1968; Thorne, 1976). These assignments and the long-obsolete

suggestions of affinities with Loranthaceae or Santalaceae were based on the incorrect assumption that Rhizophoraceae (s. str.) characteristically have an inferior ovary; on the contrary, this is a rare and derived condition in the family. Furthermore, there are many fundamental vegetative differences between Rhizophoraceae (s. str.) and all of the aforementioned groups. Suggestions of relationship with Rubiaceae, Cunoniaceae, or Dialypetalanthaceae are based solely on the common possession of interpetiolar stipules and are as indefensible as are most systematic judgments based upon a single character. Cronquist's (1981) separation of Anisophylleaceae and Rhizophoraceae and assignment of the latter to its own order, Rhizophorales, is a wiser phylogenetic policy but still begs the question of affinities. We strongly favor Dahlgren's approach that leads to the surprising but very well-supported suggestion, proposed and discussed in detail elsewhere in this volume, of affinities between Rhizophoraceae, Celastraceae, Elaeocarpaceae, and possibly several other families.

FIELD RECOGNITION OF RHIZOPHORACEAE

Because of the great infrafamilial variation in most morphological characters, the family diagnosis, given below for completeness, is unwieldy and nearly useless to both field and herbarium botanists. Much of the year the mangrove genera are easily recognized by the hypocotyls protruding from the fruits. Vegetatively, the family is recognized by having opposite (or verticillate) leaves with interpetiolar stipules; the leaves are generally bitter-tanniniferous and usually minimally toothed in inland genera. In mangal, only one nonrhizophoraceous genus has interpetiolar stipules (to only 3 mm long—the weak-stemmed Old World shrub *Scyphiphora* (Rubiaceae)). Inflorescences are axillary and basically cymose, condensed in many common genera. The sole diagnostic floral feature, present in all species of which we are aware and otherwise known only in Rhamnaceae, is that each petal (fringed in all but two genera) individually encloses either a single antipetalous stamen or a group of 2–6 stamens, depending mainly upon whether the androecium is diplostemonous or polyandrous. Rhamnaceae are easily distinguished by their isomerous stamens and entire petals and of course many other characters.

FAMILY RHIZOPHORACEAE R. BROWN

Shrubs or trees (to 50 m) of dry to wet forests or mangrove swamps; leaves opposite or verticillate, toothed, crenate, or entire. Stipules interpetiolar, valvate and pubescent or imbricate and gla-

TABLE 3. *History of tribal classifications of Rhizophoraceae (s.l.).*

This Article, 1987— Family and Tribe	Brown, 1814—Family	Endlicher, 1840—Tribe
RHIZOPHORACEAE		
(i) Rhizophoreae <i>Rhizophora</i> (1753) <i>Bruguiera</i> (1797) <i>Kandelia</i> (1834) <i>Ceriops</i> (1838)	Rhizophoreae <i>Rhizophora</i> <i>Bruguiera</i> <i>Carallia</i>	(i) Rhizophoreae <i>Rhizophora</i> <i>Bruguiera</i> <i>Kandelia</i> <i>Ceriops</i> <i>Carallia</i>
(ii) Gynotrocheae <i>Crossostylis</i> (1776) <i>Carallia</i> (1811) <i>Pellacalyx</i> (1836) <i>Gynotroches</i> (1844)		(ii) Legnotidae ² <i>Cassipourea</i> <i>Gynotroches</i>
(iii) Macarisieae <i>Cassipourea</i> ¹ (1775) <i>Macarisia</i> (1836) <i>Blepharistemma</i> (1858) <i>Dactylopetalum</i> (1859) <i>Sterigmapetalum</i> (1925) <i>Anopyxis</i> (1960) <i>Comiphyton</i> (1974)		<i>Crossostylis</i> not classified
ANISOPHYLLEACEAE		
<i>Anisophyllea</i> (1824) <i>Combretocarpus</i> (1865) <i>Poga</i> (1896) <i>Polygonanthus</i> (1932)		
Blume, ³ 1849—Family	Bentham & Hooker, 1865—Tribe	Baillon, 1876—Tribe
(i) Rhizophoreae <i>Rhizophora</i> <i>Bruguiera</i> <i>Kandelia</i> <i>Ceriops</i>	(i) Rhizophoreae <i>Rhizophora</i> <i>Bruguiera</i> <i>Kandelia</i> <i>Ceriops</i>	(i) Rhizophoreae <i>Rhizophora</i> <i>Bruguiera</i> <i>Kandelia</i> <i>Ceriops</i>
(ii) Legnotideae <i>Carallia</i> <i>Cassipourea</i> <i>Gynotroches</i>	(ii) Legnotideae <i>Carallia</i> <i>Cassipourea</i> <i>Gynotroches</i> <i>Crossostylis</i> <i>Pellacalyx</i> <i>Macarisia</i> <i>Blepharistemma</i>	(ii) Gynotrocheae (as Barraldeieae) <i>Carallia</i> <i>Gynotroches</i> <i>Crossostylis</i> <i>Pellacalyx</i>
		(iii) Macariseae <i>Cassipourea</i> <i>Macarisia</i>
	(iii) Anisophylleae <i>Anisophyllea</i> <i>Combretocarpus</i>	(iv) Anisophylleae <i>Anisophyllea</i>

TABLE 3. *Continued.*

Schimper, 1898—See Text	Ridley, ¹ 1922—Family	Melchior, 1964—Family and Tribe
I. Rhizophoroideae	(i) Rhizophoreae	RHIZOPHORACEAE
1. Gynotrocheae	<i>Rhizophora</i>	(i) Rhizophoreae
(a) Gynotrochineae	<i>Bruguiera</i>	<i>Rhizophora</i>
<i>Rhizophora</i>	<i>Kandelia</i>	<i>Bruguiera</i>
<i>Kandelia</i>	<i>Ceriops</i>	<i>Kandelia</i>
<i>Ceriops</i>		<i>Ceriops</i>
<i>Gynotroches</i>		
<i>Crossostylis</i>		
(b) Carallinae	(ii) Legnotidae	(ii) Gynotrocheae
<i>Bruguiera</i>	<i>Carallia</i>	<i>Carallia</i>
<i>Carallia</i>	<i>Gynotroches</i>	<i>Gynotroches</i>
<i>Pellacalyx</i>	<i>Pellacalyx</i>	<i>Crossostylis</i>
		<i>Pellacalyx</i>
2. Macarisieae		(iii) Macarisieae
<i>Cassipourea</i>		<i>Cassipourea</i>
<i>Dactylopetalum</i>		<i>Macarisia</i>
<i>Weihea</i>		
<i>Macarisia</i>		
<i>Blepharistemma</i>		
II. Anisophylloideae	(iii) Anisophylleae	ANISOPHYLLEACEAE
<i>Anisophyllea</i>	<i>Anisophyllea</i>	<i>Anisophyllea</i>
<i>Combretocarpus</i>		<i>Combretocarpus</i>
		<i>Poga</i>

¹ *Cassipourea* includes *Weihea*, *Lasiosepalum*, *Dactylopetalum* (p.p.), and *Petalodactylis*.

² From *Legnotis* a synonym of *Cassipourea*.

³ Miquel (1855) added *Crossostylis* and *Anisophyllea* (as *Anisophyllum*) to Legnotidae.

⁴ Non-Malaysian taxa not considered.

brous, always bearing colleters. Inflorescences axillary, cymose, dichotomous, or fasciculate. Flowers actinomorphic, bisexual or rarely unisexual, clearly articulated at juncture with pedicel. Calyx valvate, 4–many-lobed; petals equaling the number of sepals, usually with both a terminal arista and filiform appendages on the two lobes (rarely entire), each petal individually enclosing 1–5 stamens. Androecium diplostemonous to polyandrous, the filaments sometimes connate at base; nectariferous ring (“disc”) intrastaminal, entire or lobed. Ovary superior to inferior, 2–many-carpellate (locules often incompletely or not at all separated by septae at anthesis); stigma capitate or with pronounced lobes, generally papillate. Ovules 2 or many per carpel, anatropous, usually apically inserted. Fruit capsular or baccate; seeds 1–many, naked, arillate, or winged, albuminous. Embryo green, usually straight, with laminar cotyledons and epigeal germination, or with thick cotyledons (or cylindrical cotyledonary body) and viviparous germination.

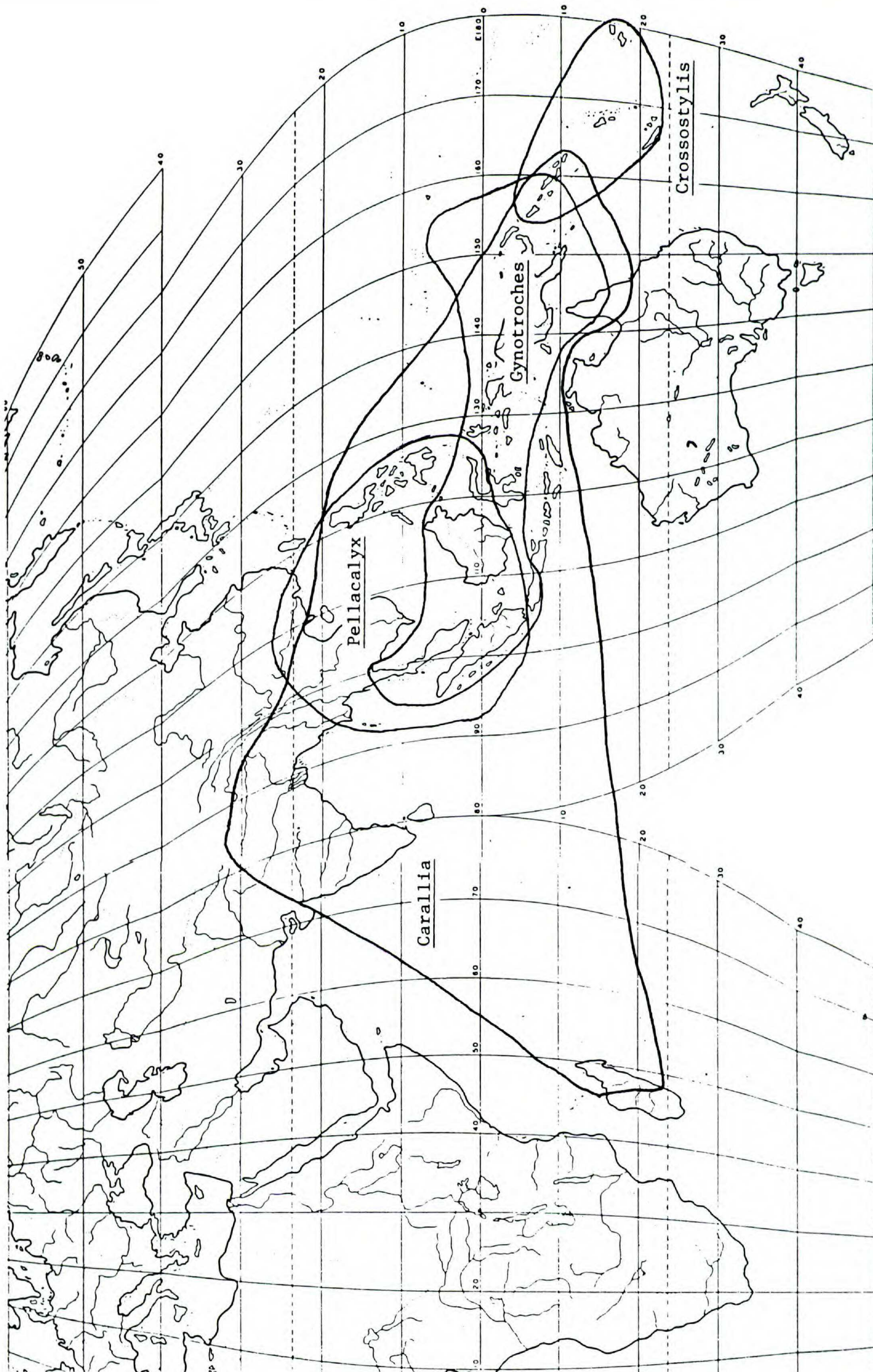
Genera. 15 (names listed by tribes); about 145 species.

Distribution. Pantropical.

In the synopsis that follows, genera are organized into the traditionally recognized tribes (e.g., Melchior, 1964), despite evidence already in hand that suggests some rearrangements (Tobe & Raven, this volume). Complete diagnoses are not given; instead, only some of the more distinctive characteristics of each tribe or genus are mentioned. References are likewise selectively cited. Listing of tribes and genera is alphabetical.

TRIBE GYNOTROCHEAE

Shrubs to large trees, some species weedy and characteristic of highly disturbed vegetation. Prominent aerial roots known in all genera but *Pellacalyx*. Leaves bijugate (not decussate), generally crenate. Stipules glabrous and imbricate (except in *Pellacalyx*). Flowers bisexual (except in *Gynotroches*); stamens twice the number of petals; ovary



inferior (except superior in *Gynotroches*), 5- or many-carpellate; ovules 2 or many per carpel (locules incompletely separated). Fruit \pm baccate, 1-many-seeded; seeds naked (except arillate in *Crossostylis*). This highly variable tribe has been the source of much confusion and is undoubtedly paraphyletic. Its proposed subdivision by Tobe & Raven (this volume) aids in clarification.

Genera. *Carallia*, *Crossostylis*, *Gynotroches*, *Pellacalyx*.

Distribution. Centered in Malesia, except *Crossostylis* (South Pacific) (Fig. 1).

Carallia Roxb., 9 species (Brandis, 1911; Ridley, 1922; Ding Hou, 1958). Figure 2.

Distribution. Indochina, Malesia, Philippines to New Guinea; *C. brachiata* also ranges to Madagascar, India, Nepal(!), S China, Solomon Islands, and N Australia.

Stilt roots reported only in *C. brachiata*. Large stalked glands (up to 5 mm) present outside stipules in several (all?) species. Inflorescences usually lax-cymose. Flowers 5-8-merous, diplostemonous, the ovary fully inferior. Seeds 1-several. Embryologically similar to Rhizophoraceae.

Crossostylis J. R. & G. Forst., about 12 species (Smith, 1981). Figures 3, 4.

Distribution. S Pacific Islands.

Inflorescences dichotomous. Largest flowers in the family (to 6 cm wide) in *C. grandiflora* (Fig. 4). Petals with very reduced appendages, even appearing entire at maturity. Stamens variable in number, sometimes basally connate and bearing odd appendages that retain the copious nectar in pendulous flowers. Ovary multicarpellate (up to about 20), nearly superior to inferior; stigma with long lobes. Fruit dehiscent or a partially dehiscent "salt-shaker" capsule.

This genus shares some characteristics (e.g., appendaged seeds) with Macarisieae, but many others with Gynotrocheae. It is placed in its own tribe, Crossostylieae, by Tobe & Raven (this volume).

Gynotroches Blume, 2-4 species (Ding Hou, 1958; Backer & Bakhuizen, 1963). Figures 5, 6.

Distribution. Burma through Malesia to Micronesia and Melanesia.

Weedy tree; branches often drooping. Plants dioecious. Inflorescences fasciculate. Flowers 4-5-merous, diplostemonous (Fig. 6). Ovary superior, 4-5-carpellate, with 3-8 ovules per locule; stigmatic lobes sometimes elongate. Fruit a berry; seeds several to many.

The most recent revision (Ding Hou, 1958) recognizes only one species (*G. axillaris* Blume) but points out that the variation in floral characters is such that with further study several distinct species will be recognized. Juncosa & Tobe (this volume) provide some details separating two of these taxa.

Pellacalyx Korth., 8 species (Ding Hou, 1958). Figure 7.

Distribution. Burma and South China to Malesia.

Some species weedy; branches often drooping. Stipules valvate, the edges folded sharply inward. Indumentum of stellate hairs, unique among Rhizophoraceae. Pairs of bracteoles fused into a toothed cup. Number of stamens and of carpels twice the number of petals, this usually 4 or 5. Each carpel or locule with 8-25 ovules.

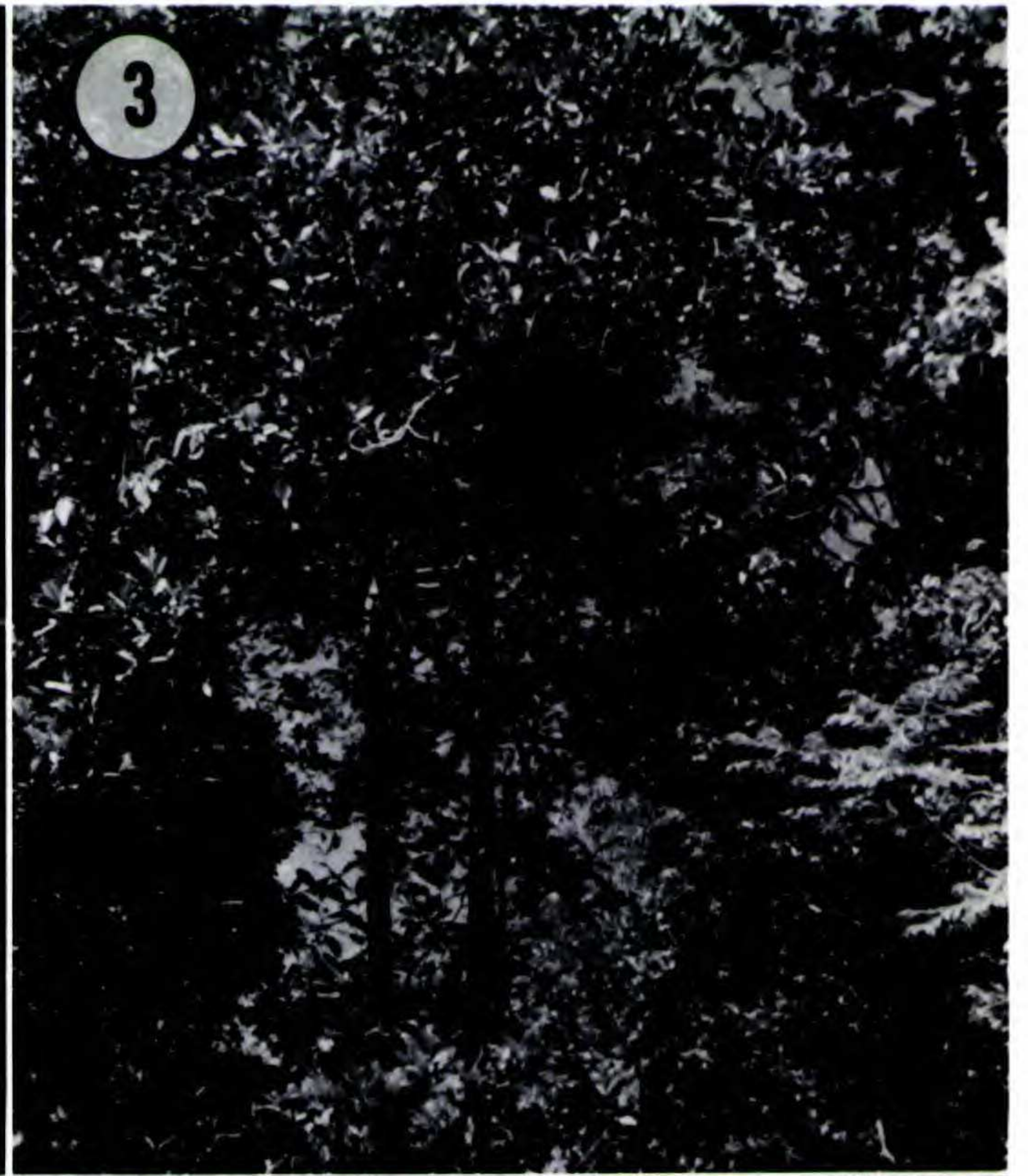
Despite its distinctive indumentum and superficially very different flowers, this genus shares many vegetative and embryological synapomorphies with *Gynotroches*; the two are clearly sister genera.

TRIBE MACARISIEAE

Shrubs to large (50 m) trees, generally of moist primary forest; but some species found in dry or deciduous forest. Stilt roots absent or weakly developed. Leaves toothed, at least in juvenile growth phases, verticillate or opposite, decussate in bud but often reoriented on branches. Stipules valvate, pubescent, also bearing colleters. Inflorescences fasciculate or lax-cymose. Flowers bisexual, except in *Sterigma petalum* and *Blepharistemma* (?). Androecium diplostemonous (polyandrous only in *Casipourea*). Ovary superior in four or five of the six genera, not in only two as sometimes stated; locules 2-6. Fruit a capsule, sometimes indehiscent; seeds arillate or winged.

Detailed information is lacking for most genera, and characterizations reported here are based largely upon the literature, much of which is very

←



incomplete and not illustrated. This basal tribe is the most poorly known group of Rhizophoraceae, largely due to the unavailability of fixed material and the rarity of certain key taxa. The three subgenera of *Cassipourea* are distinguished by several characters of calyx, androecium, and petal appendages, although three species exhibit combinations of character states of more than one subgenus (Floret, pers. comm.). *Dactylopetalum*, here re-elevated from a subgenus of *Cassipourea* to generic rank, and *Blepharistemma* are dubiously distinct at the generic level. Anatomical and monographic work in progress promises to clarify the relationships of all these arillate-seeded Macariseae. Distinctions between the winged-seeded genera (*Anopyxis*, *Macarisia*, and *Sterigmapetalum*) are clear.

Genera. *Anopyxis*, *Blepharistemma*, *Cassipourea*, *Comiphyton*, *Dactylopetalum*, *Macarisia*, *Sterigmapetalum*.

Distribution. Centered in Africa, extending to Madagascar and India (Sri Lanka) and to South and Central America (Fig. 8).

Anopyxis (Pierre) Engl., 1–3 species (Sprague & Boodle, 1909; Hutchinson & Dalziel, 1954; Irvine, 1961).

Distribution. Tropical Africa.

Tallest inland genus (to 50 m), often dominant. Leaves opposite or in whorls of 3. Calyx, petals, and ovary 5-merous. Stamens 10, filaments connate over their entire length. Petals sometimes entire. Fruit woody, indehiscent (?); seeds winged.

Blepharistemma Wall. ex Benth., 1 species (Schimper, 1898; Gamble, 1919).

Distribution. SW India.

Bracteoles absent (?); flowers polygamodioecious, 4-merous. Ovary 3-locular; fruit fleshy, indehiscent (?); seeds arillate.

Cassipourea Aublet (including subgenera *Weihea* and *Lasiosepalum*), about 55 species (Alston, 1925). Figures 9, 10.

Distribution:

subgenus *Cassipourea*: tropical Americas, West Indies, West Africa.

subgenus *Lasiosepalum*: West Africa.

subgenus *Weihea*: Africa, Madagascar, India, Sri Lanka.

Many species occurring in dry habitats; commonly shrubby, also some tall (30 m) trees (Fig. 9). Inflorescences usually condensed. Flowers (4–)5(–6)-merous. Stamens indefinite in number (15–40), in one (or more?) whorls. Ovary superior, 3(–4)-locular. Seeds 1–4; aril white, yellow, or orange.

Comiphyton Floret, 1 species (Floret, 1974, 1976).

Distribution. Gabon to E border of Zaire; not yet known from the belt defined by 2°N or S, thus one of the most narrowly equatorial ranges of any plant.

Distinguished from *Cassipourea* by its inflorescence, diplostemonous androecium, anthers, and placentation (Floret, 1974, 1976); not sharply differentiated from *Dactylopetalum*.

Dactylopetalum Benth., about 15 species (Alston, 1925; Floret, 1976).

Distribution. Equatorial Africa, Madagascar.

After consideration of remarks by Floret (1976) and other literature (Bentham & Hooker, 1865; Oliver, 1871; Dale & Greenway, 1961), we prefer to recognize this genus as distinct from *Cassipourea*; distinguishing characteristics include the diplostemonous androecium, 2-carpellate ovary, and indehiscent (?) fruit.

Macarisia Thouars, 7 species (Schimper, 1898; Arènes, 1954).

Distribution. Madagascar.

Diplostemonous, 4–5-carpellate, seeds winged.

Sterigmapetalum Kuhlmann, 7 species (Steyermark & Liesner, 1983).

←

FIGURES 2–7. *Habit and flowers of Gynotrocheae*.—2. Fully open flowers of *Carallia borneensis* growing in Brunei. Those at left opened the previous day and are now in their pistillate phase (stigmas receptive); those at right are at (staminate) anthesis.—3. *Crossostylis grandiflora* growing in New Caledonia in lowland rain forest, typical habitat for inland Rhizophoraceae.—4. Flowers of *Crossostylis grandiflora*, some at anthesis, others past. Buds are white to red, petals white.—5. *Gynotroches* sp. growing by a stream in Sarawak, E Malaysia, showing opposite bijugate leaves reoriented into one plane on horizontal or drooping branches.—6. Flowers of *Gynotroches* sp.; they were being visited (pollinated?) by numerous small ants.—7. Flowers and young fruits of *Pellacalyx cristatus* growing in Sarawak; overall habit in this genus is similar to that of *Gynotroches*.

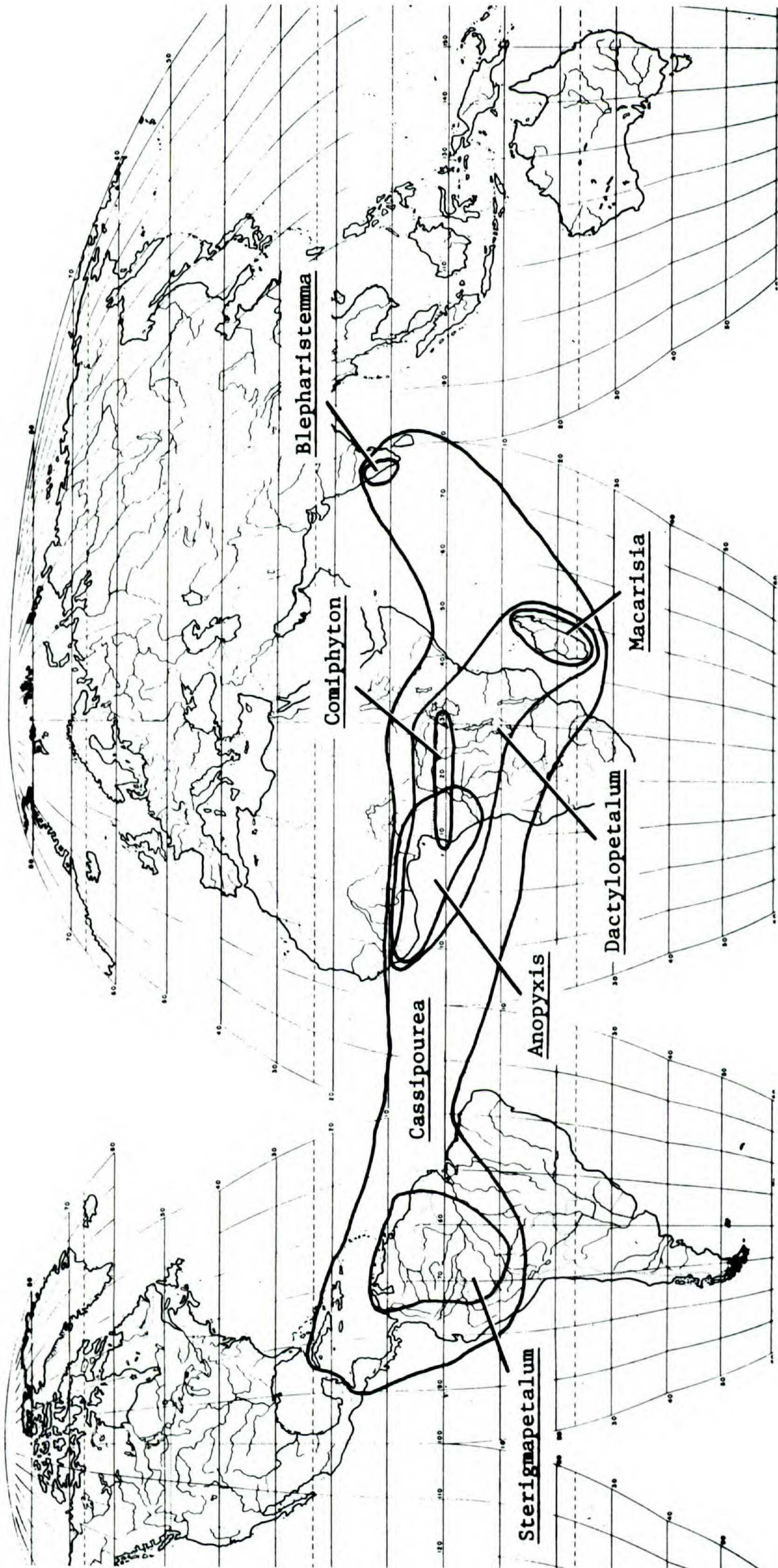
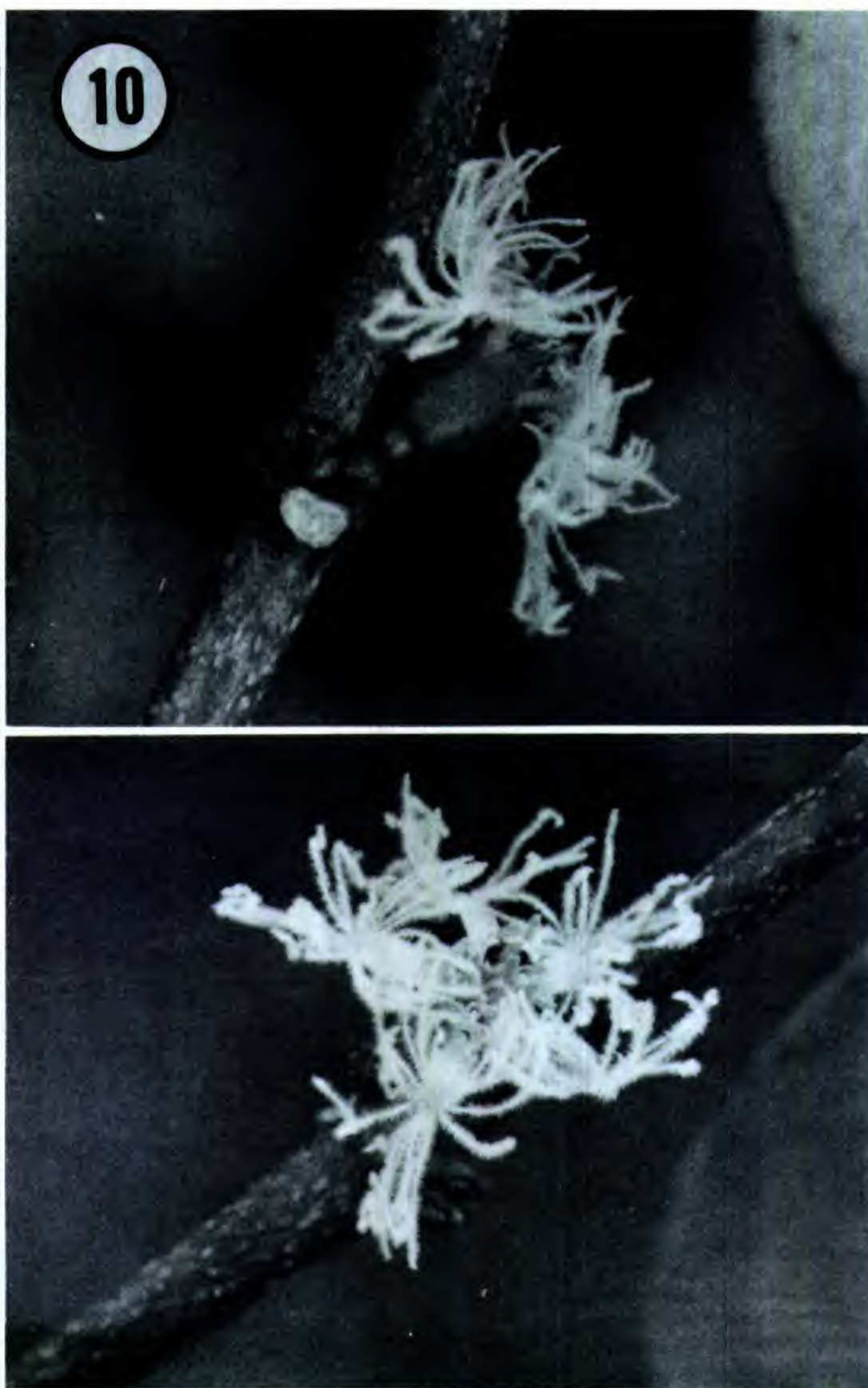
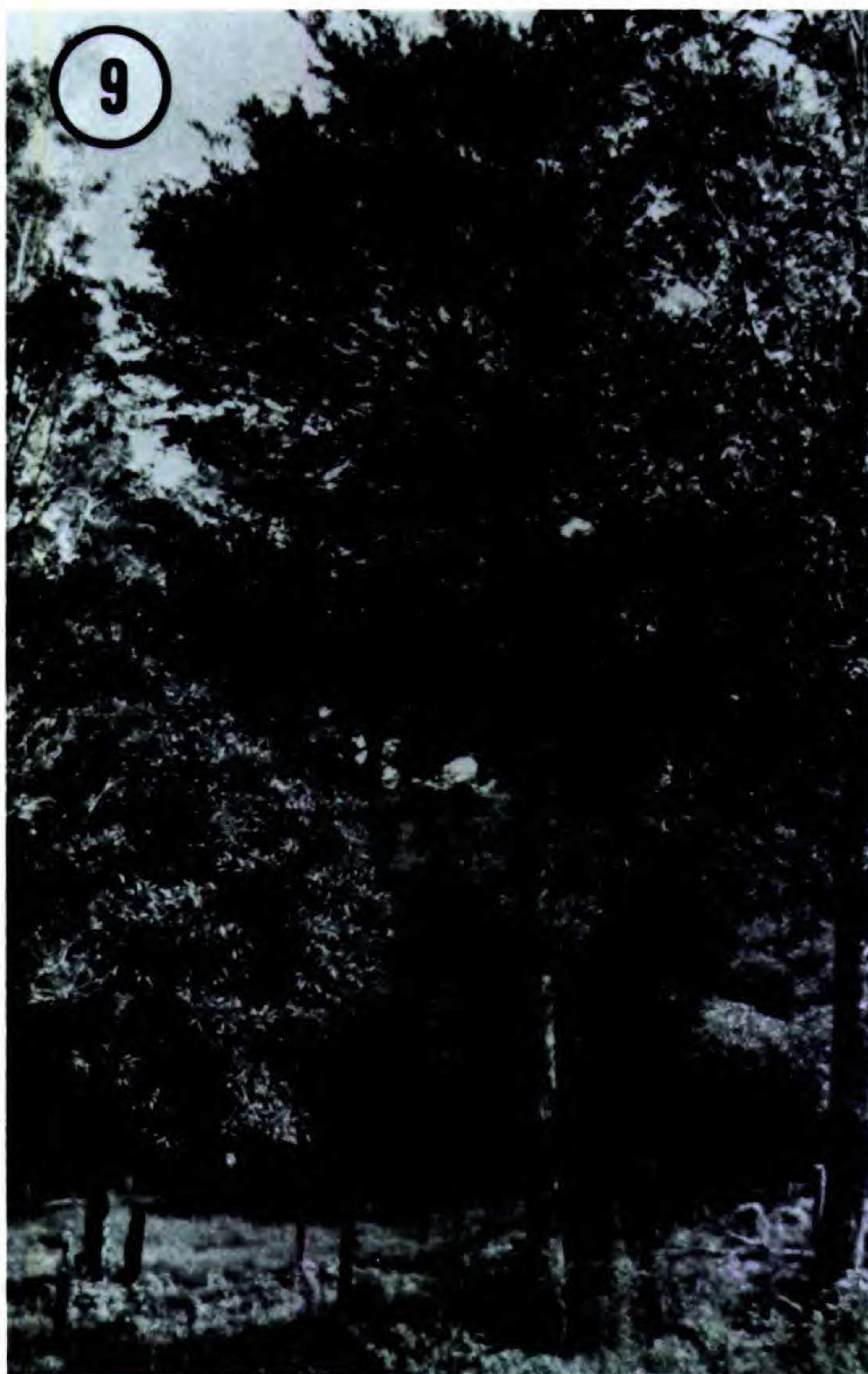


FIGURE 8. Geographical distribution of genera of Macariseae.



FIGURES 9, 10. *Habit and flower of Cassipourea (Macarisieae)*.—9. *Cassipourea* sp. growing by pasture on Monteverde, Costa Rica. Smooth unbuttressed bole and dense crown are typical of the genus.—10. Flower of *Cassipourea* sp. cf. *killipii* (Chocó, Colombia) at anthesis, showing both side and top views; plumose petal appendages greatly increase apparent size of flower.

Distribution. NW South America.

Plants dioecious. Leaves usually verticillate. Flowers 4–6-merous, diplostemonous. Seeds winged.

TRIBE RHIZOPHOREAE

Shrubs or trees of mangrove swamps; flowering plants 1.5–50 m tall. Aerial stilt roots always produced, prominent only in *Rhizophora*. Leaves entire, bijugate. Inflorescences variable, generically diagnostic. Flowers 4-multimerous, mostly diplostemonous, the petals variously specialized for diverse pollination mechanisms. Ovary half to fully inferior, 2–3-carpellate; ovules 2 per carpel. Fruit baccate, fibrous, 1-seeded. Germination viviparous, the huge seedling axis (to 1 m) emerging from both seed coat and fruit up to 9 months before abscission.

This familiar tribe is unfortunately morphologically atypical of the family; this has led to considerable confusion in phylogenetic decisions.

Genera. *Bruguiera*, *Ceriops*, *Kandelia*, *Rhizophora*.

Distribution. Pantropical (Fig. 11).

Bruguiera Lam., 6 species (Ding Hou, 1957, 1958). Figure 12.

Distribution. SE Africa through Malesia to Pacific Islands and Northern Australia.

Inflorescences cymose or reduced to 1–3 flowers, sometimes ebracteolate. Flowers polymerous, diplostemonous; ovary deeply inferior, 3-carpellate. Each petal encloses two stamens, releasing them explosively when stimulated. Petal appendages often reduced, the petals variably pubescent abaxially.

Ceriops Arn., 2 species, 1 variety (Ding Hou, 1958). Figures 13, 14.

Distribution. SE Africa through Malesia to Australia.

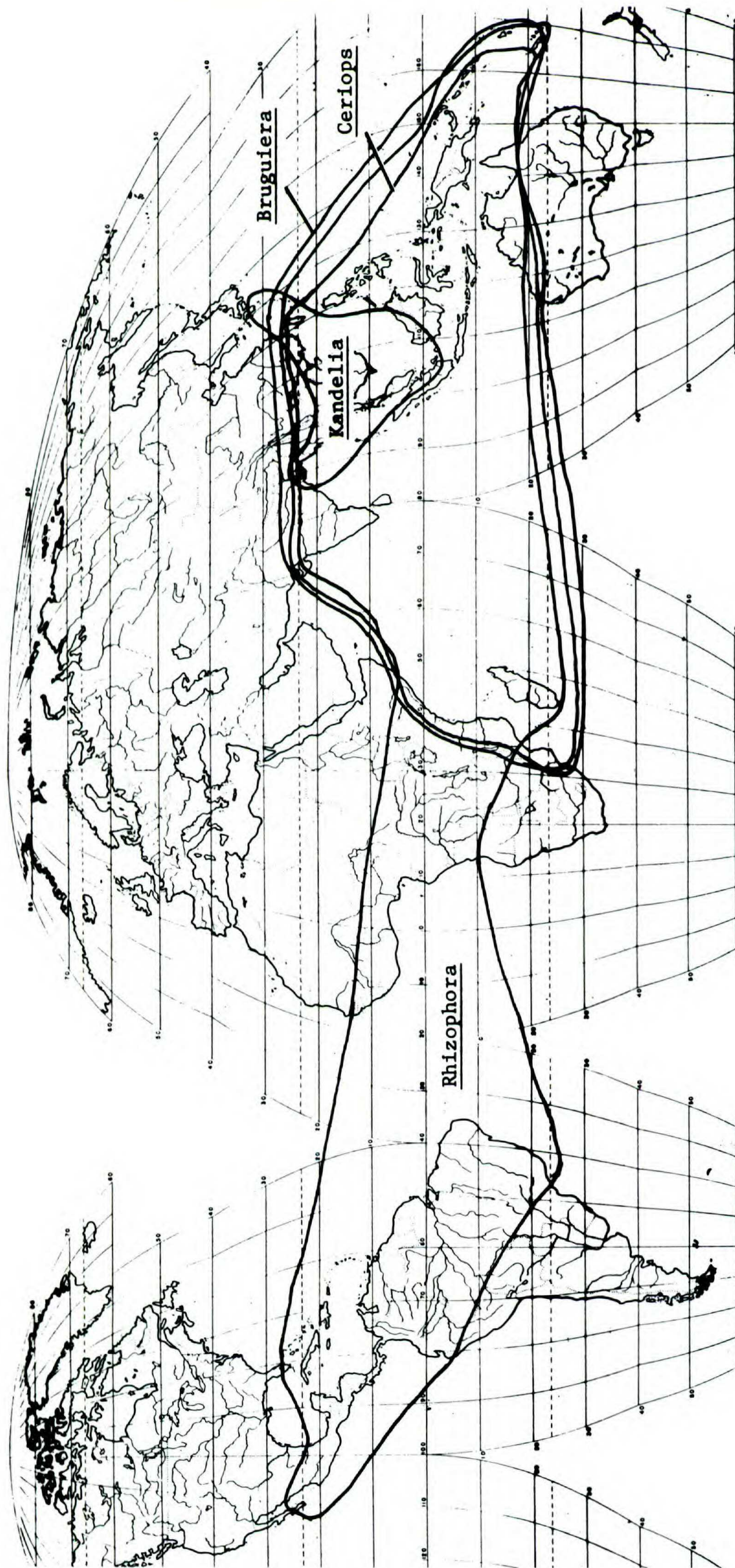
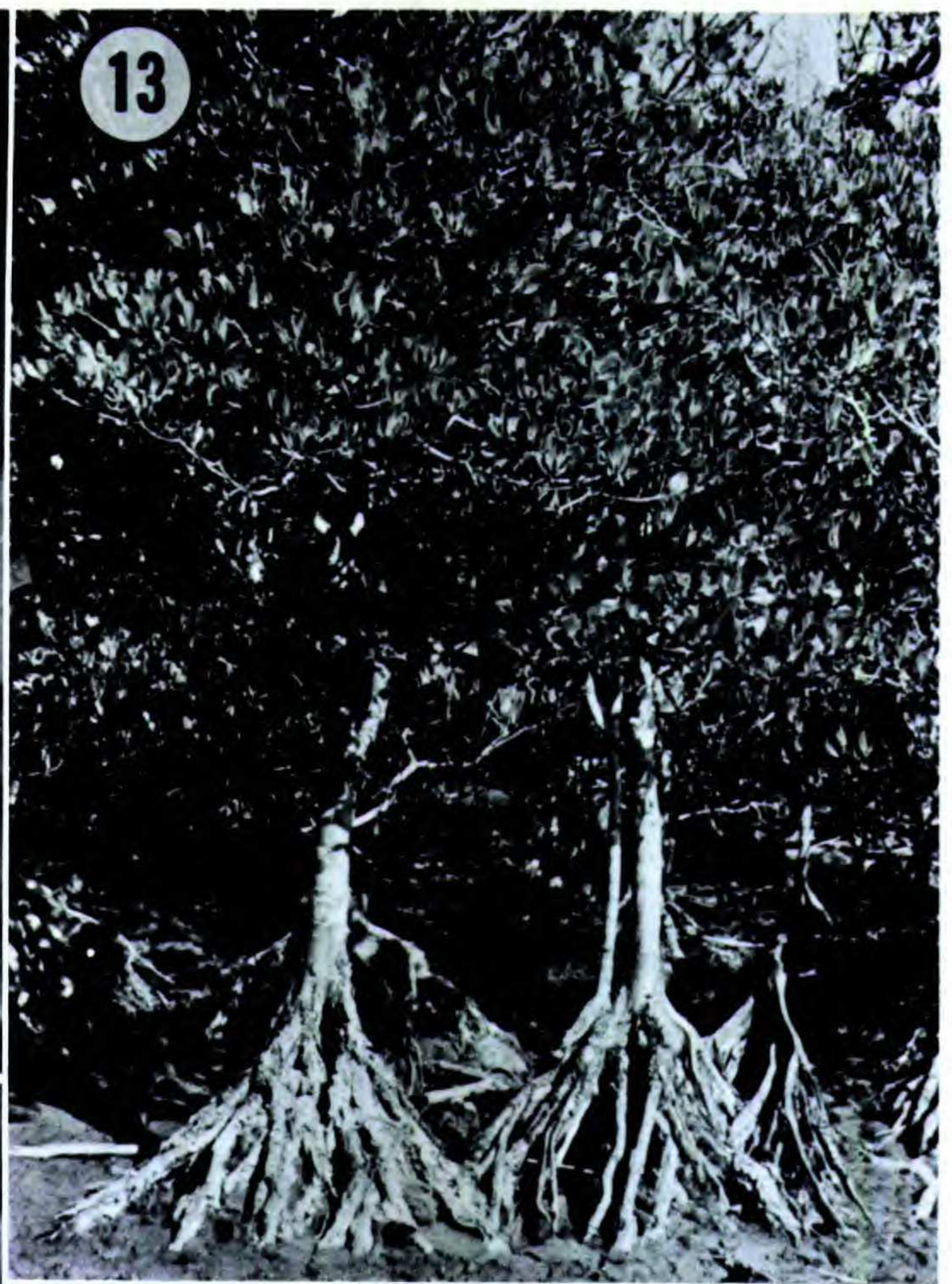


FIGURE 11. Geographical distribution of genera of tribe Rhizophoreae. Rhizophora and Bruguiera have been introduced and are becoming naturalized in Hawaii (not shown).



FIGURES 12-16. Habit, flowers, and viviparous seedlings of Rhizophoreae.—12. Flower and blunt-tipped seedling of *Bruguiera exaristata* (NW Queensland, Australia).—13. Small trees (the usual habit) of *Ceriops tagal* (Sarawak), showing low cone of stilt roots that coalesce to form buttresses; leaves of this very drought- and salt-tolerant species are curled and upright.—14. Branch tip with fasciculate inflorescences of *Ceriops tagal* (Sarawak).—15. Branch tip of *Kandelia candel* (Sarawak) with mature viviparous seedlings. The long-acuminate seedlings of this genus have a mode of establishment unlike that of other Rhizophoreae.—16. Habit of *Rhizophora apiculata* (New Caledonia). In this species, highly adapted to anemophily, flowers are borne well below leaves, and petals and dehisced stamens may abscise before the flower opens.

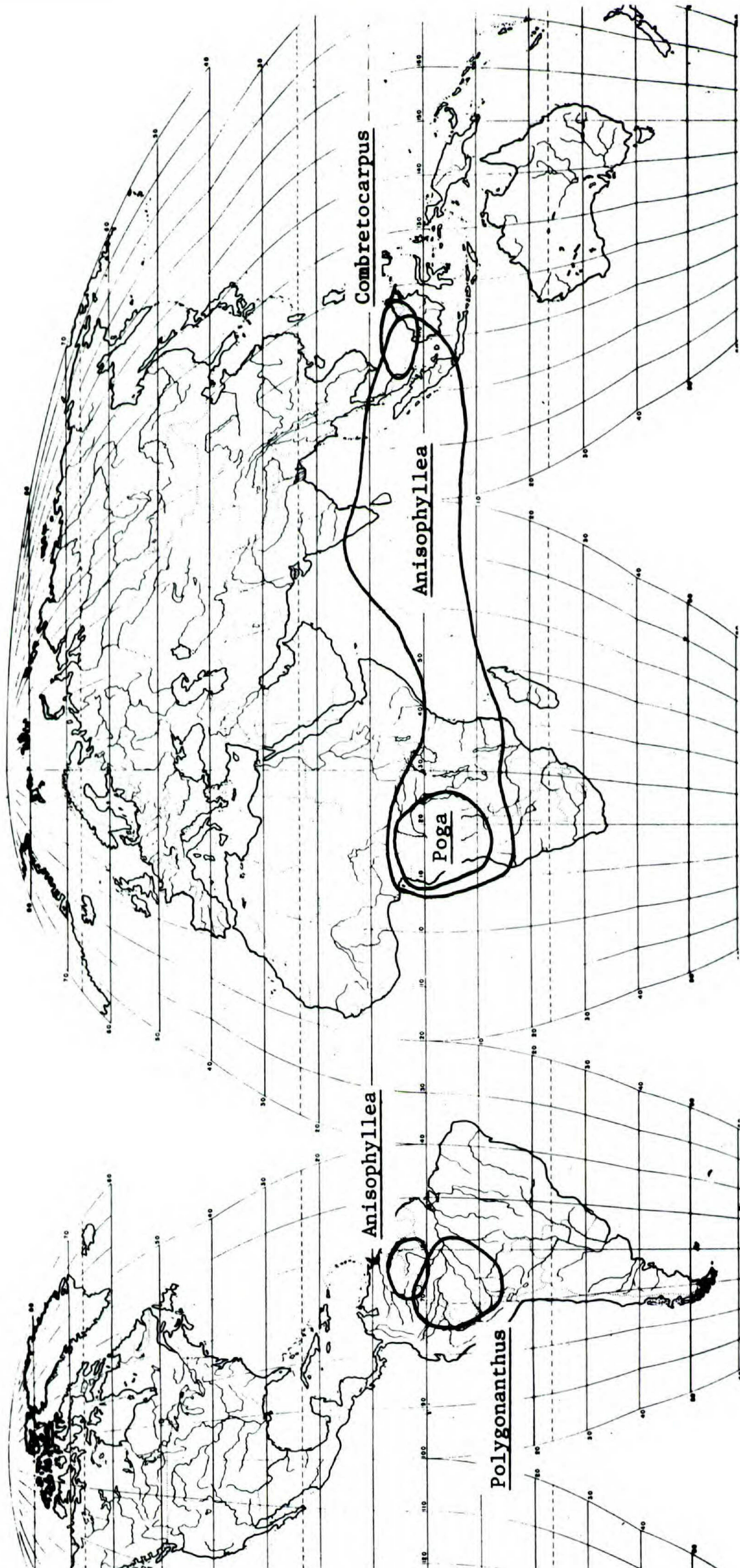


FIGURE 17. Geographical distribution of genera of family Anisophylleaceae. In Peninsular Malaysia, *Combretocarpus* may now be extinct.



FIGURES 18, 19. *Habit and inflorescence of Anisophylleaceae.*—18. *Anisophyllea disticha* (Brunei), a common understory shrub in Malaysia; large trees in this genus have similar architecture and phyllotaxis, albeit less obvious.—19. *Foliage and paniculate inflorescence of Combretocarpus rotundatus* (Also from Brunei).

Most salt-tolerant genus of the tribe; frequently shrubby; bark pale (unlike all other genera of the tribe). Inflorescences fasciculate (Fig. 14), trichasial changing to monochasial. Flowers pentamerous, diplostemonous; ovary half-inferior, 3-carpellate. Hypocotyl generally ridged.

Kandelia (DC.) Wight & Arn., 1 species (Ding Hou, 1958). Figure 15.

Distribution. Bangladesh to S Japan, through Indochina to Malaysia, Sumatra, Borneo. Characteristically found on riverbanks.

Inflorescences dichotomous; bracteoles connate and corky. Flowers 4–5-merous; petals to 2 cm, 3–7-lobed nearly to base; stamens about 30; ovary half-inferior, 3-carpellate. Hypocotyls long-acuminate.

Rhizophora L. Either 8 species or 4 species, 2 distinct varieties, 3 hybrids (Salvoza, 1936; Ding Hou, 1958; Tomlinson, 1978). Figure 16.

Distribution. Pantropical, barely extending to subtropics.

Large stilt roots. Inflorescences dichotomous, bracteoles of most species tiny. Flowers 4-merous; ovary half-inferior, 2-carpellate. Petals entire (this unique in the family) but usually densely pubescent, the edges barely enclosing each antipetalous stamen. Stamens 8, in two whorls, except 3 times the number of petals in *R. apiculata*; multilocellate in all species. Wind pollinated.

FAMILY ANISOPHYLLEACEAE RIDLEY

Trees and shrubs of wet primary forest; leaves alternate, dimorphic (except in *Combretocarpus*), exstipulate or with highly reduced stipular homologues. Inflorescences axillary, racemose to paniculate. Flowers mostly unisexual (plants monoecious), except bisexual in *Combretocarpus*. Calyx and petals valvate, 3–5-merous. Petals lobed or lacinate (except entire in *Polygonanthus*). Androecium diplostemonous. Nectary crenate. Ovary inferior, 3–

4-locular, the styles separate. Ovules 1–2 per carpel. Fruit a drupe or dry, winged (*Combretocarpus*), usually 1-seeded. Endosperm lacking; embryo with reduced or no cotyledons. Germination hypogeal.

Genera. *Anisophyllea*, *Combretocarpus*, *Poga*, *Polygonanthus*.

Distribution. South America, Africa, India to Malesia (Fig. 17).

Anisophyllea R. Brown ex Sabine, 25 species (Hutchinson & Dalziel, 1954; Ding Hou, 1958). Figure 18.

Distribution. South America, Africa, India to Malesia.

Shrubs 1.5 m tall through large trees. Axes strongly differentiated; plagiotropic branches of most species anisophyllous, with unique tetrastichous phyllotaxy (Fig. 18). Serial axillary buds numerous. Staminate and pistillate flowers either in separate inflorescences or mixed, often not strongly heteromorphic, usually 4-merous. Drupes 2–15 cm, usually 1-seeded.

Combretocarpus Hook. f., 1 species (Ding Hou, 1958). Figure 19.

Distribution. Borneo.

Large tree of peat swamps. Leaves isomorphic, distichous. Inflorescence paniculate (Fig. 19). Flowers bisexual, usually trimerous. Petals linear or irregularly 3–4-lobed. Fruit winged.

Poga Pierre, 1 species (Hutchinson & Dalziel, 1954).

Distribution. Equatorial Africa.

Large tree. Leaves anisophyllous. Inflorescences on specialized leafless branches. Flowers unisexual, strongly heteromorphic. Fruits with 3–4 edible oily seeds.

Polygonanthus Ducke, 2 species (Prance et al., 1975).

Distribution. Brazil (Amazonia).

Small trees. Leaves anisophyllous. Flowers unisexual, strongly heteromorphic; petals unlobed, nearly linear.

LITERATURE CITED

- ALSTON, A. H. G. 1925. Revision of *Cassipourea*. Kew Bull. 1925: 241–276.
- ARÈNES, J. 1954. Rhizophoracées. In: H. Humbert (editor), Flore de Madagascar et des Comores. Firmin-Didot, Paris.
- BACKER, C. A. & R. C. BAKHUIZEN VAN DEN BRINK, JR. 1963. Flora of Java, Volume 1. N. V. P. Noordhoff, Groningen, The Netherlands.
- BAILLON, H. 1876. Natural History of Plants (English edition). L. Reeve, London.
- BENTHAM, G. & J. D. HOOKER. 1865. Genera Plantarum, Volume 1, Part 2. Reeve, London.
- BLUME, C. L. 1849. Museum Botanicum. Pp. 126–131.
- BRANDIS, D. 1911. Indian Trees. Constable, London.
- BRETELER, F. J. 1969. The Atlantic species of *Rhizophora*. Acta Bot. Neerl. 18: 434–441.
- . 1977. America's Pacific species of *Rhizophora*. Acta Bot. Neerl. 26: 225–230.
- BROWN, R. 1814. General remarks, geographical and systematical, on the botany of Terra Australis. Appendix III. Pp. 533–613 in M. A. Flinders, Voyage to Terra Australis. G. & W. Nicol, London.
- CORNER, E. J. H. 1976. The Seeds of Dicotyledons. 2 Volumes. Cambridge Univ. Press, Cambridge.
- CRONQUIST, A. 1968. The Evolution and Classification of Flowering Plants. Houghton Mifflin Co., Boston.
- . 1981. An Integrated System of Classification of Flowering Plants. Columbia Univ. Press, New York.
- DAHLGREN, R. M. T. Rhizophoraceae and Anisophylleaceae: summary statement, relationships. Ann. Missouri Bot. Gard. (this volume).
- DALE, I. R. & P. J. GREENWAY. 1961. Kenya Trees and Shrubs. Buchanan's Kenya Estates, Nairobi.
- DING HOU. 1957. A conspectus of the genus *Bruguiera* (Rhizophoraceae). Nova Guinea, n.s. 8: 163–171.
- . 1958. Rhizophoraceae. Flora Malesiana, series 1, 5: 429–493.
- . 1960. A review of the genus *Rhizophora* with special reference to the Pacific species. Blumea 10: 625–634.
- DUKE, N. C. & J. S. BUNT. 1979. The genus *Rhizophora* (Rhizophoraceae) in north-eastern Australia. Austral. J. Bot. 27: 657–678.
- DUMORTIER, B. C. 1829. Analyse des Familles des Plantes avec l'Indication des Principaux Genres qui s'y Rattachent. J. Casterman, Tournay.
- ENDLICHER, S. 1840. Genera Plantarum. [Frederick] Beck, Vienna. Vindobonae.
- FLORET, J.-J. 1974. *Comiphyton*, genre nouveau gabonais Rhizophoraceae—Macarisieae. Adansonia, ser. 2, 14: 499–506.
- . 1976. A propos de *Comiphyton gabonense* (Rhizophoraceae—Macarisieae). Adansonia, ser. 2, 16: 39–49.
- GAMBLE, J. S. 1919. Flora of the Presidency of Madras, part 3. Botanical Survey of India, Calcutta.
- HUTCHINSON, J. & J. M. DALZIEL. 1954. Flora of West Tropical Africa, 2nd edition. Crown Agents for Overseas Governments and Administrations, London.
- IRVINE, F. R. 1961. Wood Plants of Ghana. Oxford Univ. Press, London.
- JUNCOSA, A. M. 1982. Developmental morphology of the embryo and seedling in *Rhizophora mangle* L. (Rhizophoraceae). Amer. J. Bot. 69: 1599–1611.
- & P. B. TOMLINSON. Systematic comparison and some biological characteristics of Rhizophoraceae and Anisophylleaceae. Ann. Missouri Bot. Gard. (this volume).
- LINNAEUS, C. 1753. Species Plantarum. L. Salvii, Stockholm.
- MACNAE, W. 1968. A general account of the fauna and flora of mangrove swamps and forests in the

- Indo-West Pacific region. *Advances Mar. Biol.* 6: 73-270.
- MARCO, H. F. 1935. Systematic anatomy of the woods of the Rhizophoraceae. *Trop. Woods* 44: 1-20.
- MELCHIOR, H. (editor). 1964. A. Engler's Syllabus der Pflanzenfamilien, 12th edition, Volume 2. Gebrüder Borntraeger, Berlin.
- MIQUEL, F. A. W. 1855. *Flora van Nederlandische Indië*. Van der Post, Amsterdam.
- OLIVER, D. 1871. *Flora of Tropical Africa*, Volume 2. L. Reeve, London.
- PRANCE, G. T., M. FREITAS DA SILVA, B. W. ALBUQUERQUE, I. DE J. DA SILVA ARAÚJO, L. M. MEDEIROS CARREIRA, M. M. NOGUEIRA BRAGA, M. MACEDO, P. N. DA CONCEICAO, P. L. BRAGA LISBÔA, P. I. BRAGA, R. C. LOBATO LISBÔA & R. C. QUEIROZ VILHENA. 1975. Revisão taxônomica das espécies amazônicas de Rhizophoraceae. *Acta Amazonica* 5: 5-22.
- RIDLEY, H. N. 1922. *The Flora of the Malay Peninsula*, Volume 1. L. Reeve, London.
- RUMPHIUS, G. E. 1741-1755. *Herbarium Amboinense*. Amsterdam.
- SALVOZA, F. M. 1936. *Rhizophora*. *Nat. Appl. Sci. Bull. Univ. Philipp.* 5: 179-237.
- SCHIMPER, A. F. W. 1898. Rhizophoraceae. *In*: A. Engler & K. Prantl (editors), *Die Natürlichen Pflanzenfamilien*. Engelmann, Leipzig.
- SMITH, A. C. 1981. *Flora Vitiensis Nova*, Volume 2. Pacific Tropical Botanical Garden, Lawai, Kauai, Hawaii.
- SPRAGUE, T. A. & L. A. BOODLE. 1909. Kokoti (*Anopyxis ealaensis*, Sprague). *Kew Bull.* 1909: 309-312.
- STEYERMARK, J. A. & R. LIESNER. 1983. Revision of the genus *Sterigmapetalum* (Rhizophoraceae). *Ann. Missouri Bot. Gard.* 70: 179-193.
- TAKHTAJAN, A. 1980. Outline of the classification of flowering plants (Magnoliophyta). *Bot. Rev. (Lancaster)* 46: 225-359.
- THORNE, R. F. 1976. A phylogenetic classification of the Angiospermae. *Evol. Biology* 9: 35-106.
- TOBE, H. & P. H. RAVEN. Seed morphology and anatomy of Rhizophoraceae, inter- and infrafamilial relationships. *Ann. Missouri Bot. Gard.* (this volume).
- TOMLINSON, P. B. 1978. *Rhizophora* in Australasia—some clarification of taxonomy and distribution. *J. Arnold Arbor.* 59: 156-169.
- . 1986. *The Botany of Mangroves*. Cambridge Univ. Press, Cambridge.
- VLIET, G. J. C. M. VAN. 1976. Wood anatomy of the Rhizophoraceae. *Leiden Bot. Ser. No.* 3: 20-75.
- WILLIS, J. C. 1973. *A Dictionary of the Flowering Plants and Ferns*, 8th edition (revised by H. K. Airy Shaw). Cambridge Univ. Press, Cambridge.